Spatial variability in the soil macroinvertebrate food web of an agroecosystem: a stable isotope analysis

MSc Thesis

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Author contributions

This work is part of the project "Multitrophic interactions in the arthropod community of an organic citrus grove", funded by the Spanish government (MCyT; CGL2010-18182/BOS) and whose principal researcher is Josep Piñol.

The author started working on this project at the beginning of 2013 and continues at present. Part of the research performed to date has been used to develop this work. All his activities have been supervised by Prof. Josep Piñol and Prof. Xavier Espadaler.

Josep Piñol (JP) and Xavier Espadaler (XE) formulated the idea. JP, XE and Carlos Hernández-Castellano (CHC) defined and discussed the experimental design. CHC, JP and XE performed the field work. CHC identified plant specimens. XE, other collaborators (see Acknowledgements) and CHC identified animal specimens. CHC processed animal, plant, and soil samples. CHC prepared the database, performed statistical analyses, reviewed the literature and wrote the manuscript.

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Abstract

Although trophic structure and feeding preferences of soil macroinvertebrates can change among habitats, the extent to which food web structure varies within ecosystems is unknown. In this work we aimed to assess changes in food web structure in an agroecosystem using an experiment setting in which plant and macroinvertebrate community composition and stable isotopes (δ^{13}C and δ^{15}N) of soil, plants and macroinvertebrates were analyzed at increasing distances from trees within a citrus grove and in an adjacent abandoned field. Within the citrus grove the macroinvertebrate community near the trunk differed from that located further away because of a higher number of detritivores. Generally, δ^{13}C and δ^{15}N values of soil, plants and macroinvertebrates decreased at increasing distances from trees. After correcting isotope values of macroinvertebrates by their isotopic baselines, macroinvertebrates

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from the abandoned field presented lower δ^{15}N values than those of the citrus grove (*i.e.* they fed on lower trophic positions), and within the citrus grove macroinvertebrates near the trunk presented lower δ^{13}C than those of the treatments further away (*i.e.* they relied more in plant-based resources). Decreasing organic matter and water availability at increasing distances from trees is the most parsimonious explanation of the observed isotopic gradient, and may in turn drive changes in food web structure (composition and trophic positions of species) in the studied area, both within the citrus grove and between the citrus grove and the abandoned field. Therefore, food web studies must take into account within-habitat heterogeneity when determining sampling scale and food web-related ecosystem processes.

Keywords

δ^{13}C; δ^{15}N; arthropod community; trophic structure; trophic shift

Introduction

Soil, which is the ultimate destination of around 90% of the terrestrial net primary production, harbours a great diversity of organisms responsible for decomposition and nutrient cycling in ecosystems (Coleman et al. 2004). Their trophic relationships are depicted as food webs, which present the energy pathway from decomposers to predators and where high rates of omnivory are normally present (Moore and de Ruiter 1991; Scheu 2002). The formalization of such complex structures has been traditionally based on direct observations. However, observational data are difficult to gather in soil

43 communities because of the size and habits of species, and even occasional observations
44 might not be truly representative of the long-term relationship between two species.

45 The analysis of stable isotopes ratios of C and N (δ^{13}C and δ^{15}N) is an alternative
46 approach that integrates information over time on trophic positions, trophic links with
47 community members and sources of energy used by animals (Tiunov 2007). Both δ^{13}C
48 and δ^{15}N increase with trophic level because of the fractionation process that enriches
49 the consumer in the heavy isotope in relation to its diet (trophic enrichment). While the
50 increase in δ^{13}C is low (0.5±0.1‰) and, therefore, useful to infer potential food sources,
51 the increase in δ^{15}N is larger (2.3±0.2‰) and can be used as an estimator of trophic
52 position (McCutchan et al. 2003). Overall, the isotopic variance of a population can be
53 used as a proxy of the species niche width (Bearhop et al. 2004), and it has been useful
54 to depict trophic relationships between the soil food web components (*e.g.* Scheu and
55 Falca 2000; Ponsard and Arditi 2000).

56 The role of macroinvertebrates in decomposer food webs is very important. Besides
57 being ecosystem engineers responsible of soil structure formation, they process large
58 amounts of litter, producing faeces that stimulates the microbial activity and, therefore,
59 decomposition (Hättenschwiler et al. 2005). Thus, knowing to what extent the food web
60 structure varies spatially can shed light into the drivers that ultimately determine the
61 ecosystem functioning (Ettema and Wardle 2002). In this regard, stable isotopes have
62 been proven to be useful to study trophic structure shifts of macrodecomposers between
63 managed and abandoned pastures (Seeber et al. 2005), and to show that concrete groups
64 of arthropods or whole communities can change their feeding habits among habitats
65 (Gibb and Cunningham 2011; Klarner et al. 2014). However, the extent to which soil
66 macroinvertebrate food web structure change within the same ecosystem is unknown.
67 Moreover, there is scarce information of stable isotope research in agroecosystems and,

when present, the whole macroinvertebrate community is seldom analyzed. Therefore, knowing at what scale changes in soil macroinvertebrate community composition and trophic structure are present may help understand key ecosystem processes and the scale at which these studies should be conducted.

We live in an heterogeneous world, and even within the same ecosystem it is expected some spatial variability in resources, thus leading to possible changes in food web structure at small scales. In this work we aim to assess the spatial variability in the soil macroinvertebrate food web structure of a Mediterranean agroecosystem. In particular, we want to study: i) the influence of spatial variability in resources in the macroinvertebrate community composition; ii) how and at what scale the environment influences the trophic structure of macroinvertebrates; and iii) how trophic structure differs across space between the delimited food webs. To do so we take advantage from a marked gradient in resource availability (organic manure and irrigation) from the trees in a citrus grove to a nearby abandoned field. Throughout this gradient we: i) analyzed plant and macroinvertebrate community composition; ii) analyzed stable isotopes of soil, plant and macroinvertebrates; and iii) over the delimited food webs we identified trophic groups of species and calculated several metrics of trophic diversity and trophic redundancy.

Materials and methods

Study site

The study was conducted in an organic citrus grove and a nearby abandoned field located at La Selva del Camp (Tarragona, NE Spain; 41º13'07"N, 01º08'35"E). The grove consists of ca. 300 Clementine trees (*Citrus clementina* var. *clemenules*) grafted

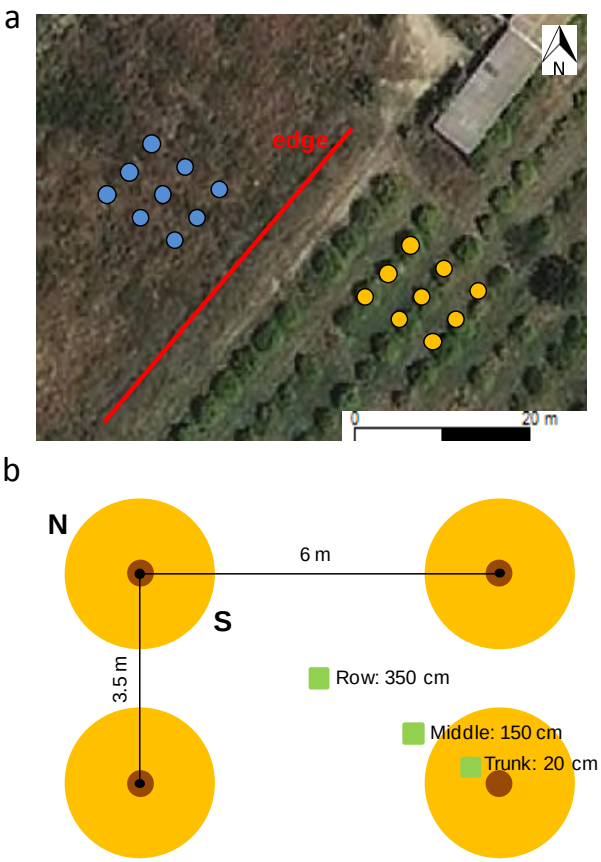
on the hybrid rootstock Carrizo citrange (*Poncirus trifoliata* (L.) Raf. x *Citrus sinensis* (L.) Osb.). Trees are watered twice a week during dry periods and fertilized each year with organic manure. Grasses and other weeds form a permanent ground cover, which is mowed three or four times a year. The abandoned field is adjacent to the citrus grove. The edge consists on a smooth ravine with shrubs and some fruit trees. It was cultivated until 2003 and now is entirely covered by forbs, grasses and small shrubs, which are mowed once a year.

Experimental design

We set up an experiment to study the spatial variability in plant and macroinvertebrate communities and in stable isotope signatures of soil, plants and macroinvertebrates. We did that on a small scale and on a mesoscale. On the small scale we set three different treatments within the citrus grove at increasing distance from the tree trunk, where irrigation and fertilizer is applied: Citrus:Trunk (20 cm to the tree trunk), Citrus:Middle (150 cm), Citrus:Row (350 cm) (total: 9 trees; 27 samples, S-N oriented). On the mesoscale we compared the citrus grove with the abandoned field: Abandoned (ca. 30 m from the trees). We selected 9 sampling units in the abandoned field, in a layout similar to the trees in the citrus grove and at a minimum distance of ca. 5 m from the edge. Fig. 1 shows the experimental design layout.

Fig. 1 a) Location of the sampling units in the citrus grove (orange dots: selected trees) and in the abandoned field (blue dots), were samples of soil, plant and macroinvertebrates were taken. The edge between the citrus grove and the abandoned field is shown. Samples were taken at 20, 150 and 350 cm from each selected tree in the citrus grove (see b) for details). Samples in the abandoned field are at a distance of ca. 30 m from the trees in the citrus grove. b) Sampling details within the citrus grove. The brown circle represents the tree trunk and the orange one the canopy. Green squares are the surfaces where samples were taken. Distance between trees of the same row is 3.5m, and between rows is 6m. Note that samples are S-N oriented. Image (a) provided by Google Earth.

Fig. 1



152 *Sampling details*

153 Samples were collected in July 2013 between 6 a.m. and 10 a.m. Each sample consisted
154 of an area of 25x25 cm, on which the aerial part of plants were collected and preserved
155 in dry paper until identification and processing. We dug to a depth of 15 cm and
156 extracted the bulk of soil. Macroinvertebrates were collected with pincers and
157 entomological aspirators and immediately preserved in 70% ethanol. For each sample
158 we also kept 1 kg of soil for future analysis.

159 We realized that the soil was very compact at the abandoned field, so we watered
160 sampling areas and their surroundings (comprising 50x50 cm) 10 hours before sampling
161 in order to facilitate soil digging. For this reason, as it was possible that the animal
162 community changed overnight, we proceed conservatively and avoided the abandoned
163 field data in community composition analyses and used for stable isotope analyses only
164 the most abundant species.

165 We also collected citrus leaves from each sampled tree within the citrus grove and
166 samples of the fertilizer applied over the last three years (2011, 2012, 2013) beneath the
167 tree canopy. Fertilizer of 2013 had a different composition from those of the other years
168 because of an obligate change of provider.

169 *Sample processing and stable isotope analysis*

170 Soil samples were milled and sieved to 0.2 mm and pulverized on a mortar grinder. We
171 analyzed organic matter by oxidation and eliminated inorganic carbon by acid from soil
172 following Hesse (1971) and Midwood and Boutton (1998), respectively.

173 Plants were identified using a reference collection (Kindermann 2010) of the studied
174 area and with keys from Bolòs et al. (2005). We selected for isotopic analyses those

175 species accounting for the 90% of total biomass of each sample, and homogenized them
176 to a fine powder with a mixer mill.

177 Macroinvertebrates were identified to the species level when possible. We selected for
178 isotopic analyses those edaphic species with individuals of the same stage present at
179 least in two samples of a treatment (for ants we consider a nest as present if there were
180 at least 25 individuals).

181 We weighted 8-10, 1-1.5 and 0.2-2.5 mg of processed soil, plant and macroinvertebrate,
182 respectively, into tin capsules for stable isotope analyses. If a macroinvertebrate
183 specimen weighted more than 2.5 mg we homogenised it to a fine powder with a pestle.
184 For snails and earthworms we analyzed muscle tissue. Samples were dried between 24-
185 48 hours at 60ºC.

186 We analyzed $\delta^{13}C$ and $\delta^{15}N$ from all samples at the Stable Isotopes Analysis Lab
187 (LAIE), at the Autonomous University of Barcelona, using a continuous-flow Delta V
188 Advantage Isotope Ratio Mass Spectrometer, coupled to a Flash 1112 elemental
189 analyzer (both from Thermo Fisher Scientific Inc., Waltham, MA USA). Samples were
190 standardized to IAEA-600 (caffeine, $\delta^{15}N$: 1.0‰ ± 0.2 SD; $\delta^{13}C$: -27.771‰ ± 0.043 SD)
191 from International Atomic Energy Agency (Vienna, Austria). Carbon and nitrogen
192 isotope ratios were calculated relative to VPDBee and atmospheric air, respectively, and
193 expressed as ‰.

194 *Data analyses*

195 Analyses aimed to test for differences on the small scale (i.e. treatments within the
196 citrus grove) followed a randomized block design, with treatment as fixed factor and
197 tree as a random factor. On the mesoscale (i.e. citrus grove vs abandoned field) we

198 performed an assymetrical design, with treatment as fixed factor and block (trees from
199 the citrus grove and abandoned field) as a random factor nested in treatment.

200 For plant and macroinvertebrate community composition analyses we used biomass and
201 abundance data from each treatment, respectively. Raw data was first square-root
202 transformed, and a permutational multivariate ANOVA was performed using the Bray-
203 Curtis similarity index. If differences in the community composition among treatments
204 were significant, we ran a posteriori pairwise comparisons. If there were no differences
205 between pairs of treatments within the citrus grove we pooled the treatments together
206 for future comparison with the abandoned field.

207 In the rest of analyses the statistical procedure was similar, but Euclidean distance was
208 used instead and Monte Carlo *p*-values were generated when there were not enough
209 permutations. *P*-values were adjusted when multiple comparisons were > 5 following
210 the False Discovery Rate (FDR) method in R.

211 For stable isotope analyses we compared signatures of soil, plant and
212 macroinvertebrates among treatments. As we were interested in changes of the whole
213 community, we included species as a random factor nested in family and trophic guild
214 for plants and macroinvertebrates, respectively. The trophic guild of macroinvertebrates
215 was defined according to literature (Armengol 1986, Blas 1987, Altaba and Ros 1991,
216 Lövei and Sunderland 1996, Deckle and Fasulo 2001, Zimmer 2002, Bell et al. 2007,
217 Gómez and Espadaler 2007, Krantz and Walter 2009).

218 For macroinvertebrate food web structure we run an ANCOVA on macroinvertebrate
219 stable isotope signatures with soil $\delta^{13}C$ and $\delta^{15}N$ as covariates to correct community
220 signature by its baseline and to study if trophic shifts were present among treatments.

We also delimited food webs based on structural and functional criteria (see Post et al. 2007), and for each one we built ellipses of isotopically similar macroinvertebrates (trophic groups), conducting pairwise comparisons between species bivariate $\delta^{13}C$ and $\delta^{15}N$ within each trophic guild (Electronic Supplementary Material (ESM) Table S5), and adjusting the level of significance by setting a conservative threshold of $P < 0.01$. We included in this analysis those species with $n \geq 4$ to get a reasonable test. The rest of them were assigned to the closest trophic group. Trophic levels (TL) were calculated with the formula $TL = 2 + (\delta^{15}N_{top\ predator} - \delta^{15}N_{baseline}) / \Delta\delta^{15}N$ (Post 2002), where 2 is the TL of the primary consumer used to estimate the baseline ($\delta^{15}N_{baseline}$), $\delta^{15}N_{top\ predator}$ is the $\delta^{15}N$ of the top predator in the food web, and $\Delta\delta^{15}N$ is the increase in $\delta^{15}N$ per trophic level (2.3‰; McCutchan et al. 2003).

Finally, we calculated Layman's community-wide metrics of trophic structure (Layman et al. 2007). We used a Bayesian approach to these metrics with the SIBER tool (Stable Isotope Bayesian Ellipses in R) contained in the SIAR package (Stable Isotope Analysis in R v.4.2; Parnell and Jackson 2013).

Analyses were run with the software PERMANOVA+ for PRIMER v.6 (Anderson et al. 2008), with the exception of community-wide metrics, that were run in R (R Core Team, 2015).

Results

Plant and arthropod community composition

Plant community composition (ESM Table S1) changed across treatments within the citrus grove (pseudo-$F_{2,16} = 6.14$, $P = 0.0003$). Trunk was different from Middle and

Row (t = 2.64, P = 0.0063; t = 2.84, P = 0.0031; respectively), but no differences between Middle and Row were found (t = 1.18, P = 0.24). At a mesoscale (citrus grove vs abandoned field) the plant community was also different (pseudo-$F_{2,17}$ = 3.21, P = 0.0007), being both citrus grove communities different from that of the abandoned field (t = 1.45, P = 0.0001; t = 1.63, P = 0.0001; respectively).

Within the citrus grove, Trunk was dominated by *Parietaria officialis* (Urticaceae) (60.1% of all biomass), whereas Middle+Row was characterized by the presence of several grasses (75.7%), mainly *Avena barbata*, *Hordeum murinum* and *Cynodon dactylon*. In the abandoned field grasses were also abundant (20.3% of all biomass), but other species such as *Medicago* sp. (Leguminosae, 26.4%), *Dittrichia viscosa* and *Carduus pycnocephalus* (Compositae, 43.1%) conformed the vast majority of plant biomass. Total biomass was higher in the abandoned field (631 ± 77 $g \cdot m^{-2}$) than in the citrus grove (234 ± 20 $g \cdot m^{-2}$) (Fig. 2a).

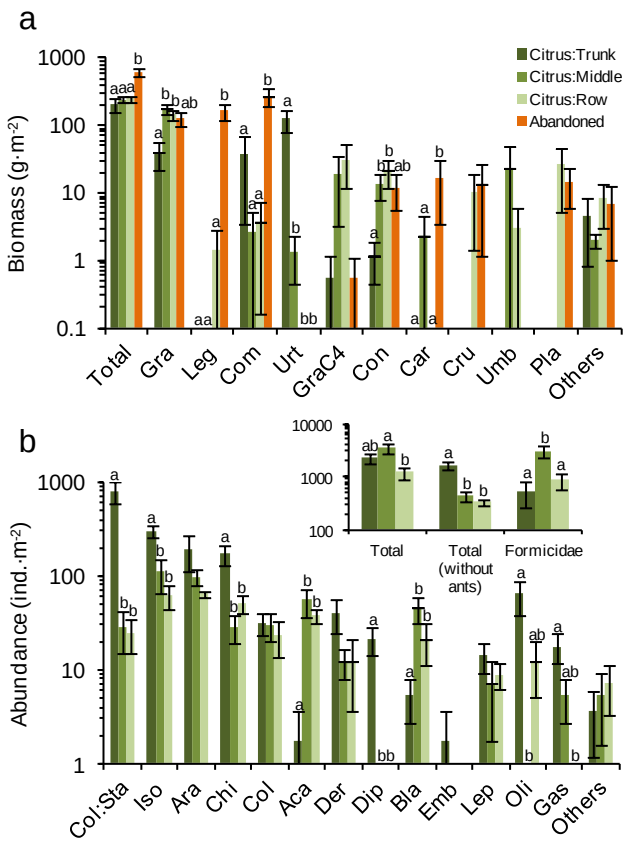
Macroinvertebrate community composition (ESM Table S2) also changed across treatments within the citrus grove (pseudo-$F_{2,16}$ = 5.48, P = 0.0001). As in plants, Trunk was different from Middle and Row (t = 2.65, P = 0.0014; t = 2.75, P = 0.0012; respectively), with no differences between Middle and Row (t = 1.48, P = 0.053).

The Trunk macroinvertebrate community was characterized by a high abundance of staphylinid beetles (mainly Aleocharinae), isopods (*Armadillidium vulgare* and *Porcellio* sp.), chilopods (*Geophilus* sp. and *Lithobius* sp.) and from the exclusive presence of the diplopod *Polydesmus* sp. In contrast, Erythraeidae mites and cockroaches (*Loboptera decipiens*) were more abundant in Middle+Row. Earthworms and snails were relatively more abundant in Trunk, whereas ants were concentrated in Middle. Without taking into account ants (social individuals aggregated in nests) total

abundance was higher in Trunk (1666 ± 260 individuals·m^{-2}) than in the rest of treatments within the citrus grove (376 ± 46 individuals·m^{-2}) (Fig. 2b).

Fig. 2 a) Plant biomass ($g \cdot m^{-2}$) and b) macroinvertebrate abundance ($individuals \cdot m^{-2}$) in each treatment (mean ± SE). For each treatment n = 9. Key for plants: Gra, Gramineae; Leg, Leguminosae; Com, Compositae; Urt, Urticaceae; GraC4, Gramineae (C_4); Con, Convolvulaceae; Car, Caryophyllaceae; Cru, Cruciferae; Umb, Umbelliferae; Pla, Plantaginaceae. Key for macroinvertebrates: Col:Sta, Coleoptera: Staphylinidae; Iso, Isopoda; Ara, Araneae; Chi, Chilopoda; Col, Coleoptera; Aca, Acari; Der, Dermaptera; Dip, Diplopoda; Bla, Blattodea; Emb, Embioptera; Lep, Lepidoptera (larvae); Oli, Oligochaeta; Gas, Gasteropoda. Shared letters and no letters mean no differences between treatments ($P > 0.05$). Note the log scale used in the graphics. Macroinvertebrate community composition data from the abandoned field was excluded in the analysis (see Materials and Methods section).

Fig. 2


a
Biomass (g·m-2)
1000
100
10
1
0.1
Citrus:Trunk
Citrus:Middle
Citrus:Row
Abandoned
Total
Gra
Leg
Com
Urt
GraC4
Con
Car
Cru
Umb
Pla
Others
b
Abundance (ind.·m-2)
10000
1000
100
1
Total
Total (without ants)
Formicidae
Col:Sta
Iso
Ara
Chi
Col
Aca
Der
Dip
Bla
Emb
Lep
Oli
Gas
Others

328 *Stable isotope signatures of soil, plants and macroinvertebrates*

329 There were no differences in soil $\delta^{13}C$ within the citrus grove (pseudo-$F_{2,16}$ = 2.03, P =
330 0.16). In contrast, there were significant decreasing values of $\delta^{15}N$ at increasing
331 distances from the tree trunk (pseudo-$F_{2,16}$ = 104.53, P = 0.0001). The citrus grove had
332 higher $\delta^{13}C$ than the abandoned field (pseudo-$F_{1,26}$ = 20.37, P = 0.0016), that presented
333 the smaller $\delta^{15}N$ among treatments (pseudo-$F_{3,8}$ = 71.95, P = 0.0001) (Fig. 3).

334 Within the citrus grove soil organic matter content (%) was 7.7±0.6, 4.3±0.6 and
335 3.6±0.2 in Trunk, Middle and Row, respectively, whereas in the abandoned field was
336 2.2±0.02 (n=4 in all treatments).

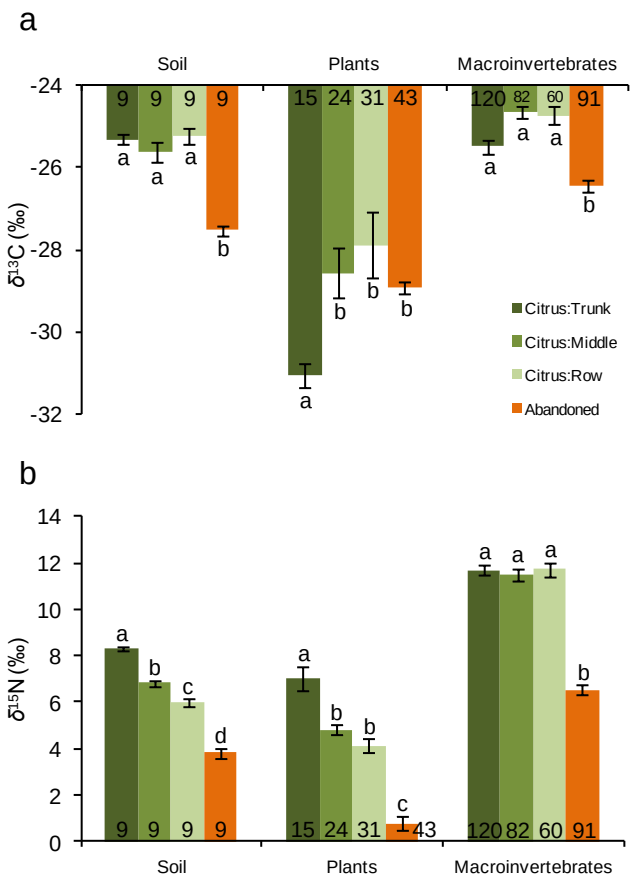
337 Plants had different $\delta^{13}C$ and $\delta^{15}N$ among treatments within the citrus grove (pseudo-
338 $F_{2,43}$ = 14.19, P = 0.0001; pseudo-$F_{2,43}$ = 7.88, P = 0.0012; respectively). Trunk had the
339 lowest $\delta^{13}C$ and the highest $\delta^{15}N$, and no differences in isotopic signatures were found
340 between Middle and Row. At mesoscale (citrus grove vs abandoned field) differences in
341 both $\delta^{13}C$ and $\delta^{15}N$ persisted (pseudo-$F_{2,63}$ = 12.55, P = 0.035; pseudo-$F_{2,63}$ = 17.04, P
342 = 0.035; respectively). The abandoned field presented higher $\delta^{13}C$ than Trunk and the
343 lowest $\delta^{15}N$ among treatments (Fig. 3).

344 For macroinvertebrates, there were no differences in either $\delta^{13}C$ or $\delta^{15}N$ values among
345 treatments within the citrus grove (pseudo-$F_{2,213}$ = 0.23, P = 0.79; pseudo-$F_{2,213}$ = 2.02,
346 P = 0.14; respectively). However, the macroinvertebrate community in the citrus grove
347 showed higher values in both $\delta^{13}C$ and $\delta^{15}N$ than that of the abandoned field (pseudo-
348 $F_{1,298}$ = 4.78, P = 0.0001; pseudo-$F_{1,298}$ = 175.49, P = 0.0001; respectively) (Fig. 3).

349 ESM Table S3 and S4 contain the complete list of stable isotope signatures for soil,
350 plants and macroinvertebrates.

Fig. 3 a) $\delta^{13}C$ and b) $\delta^{15}N$ (mean ± SE) of soil, plants and macroinvertebrates in the different treatments within the citrus grove and in the abandoned field. Shared letters mean no differences between treatments ($P > 0.05$). Sample sizes (n) are given at the bottom of each graphic bar.

377 **Fig. 3**



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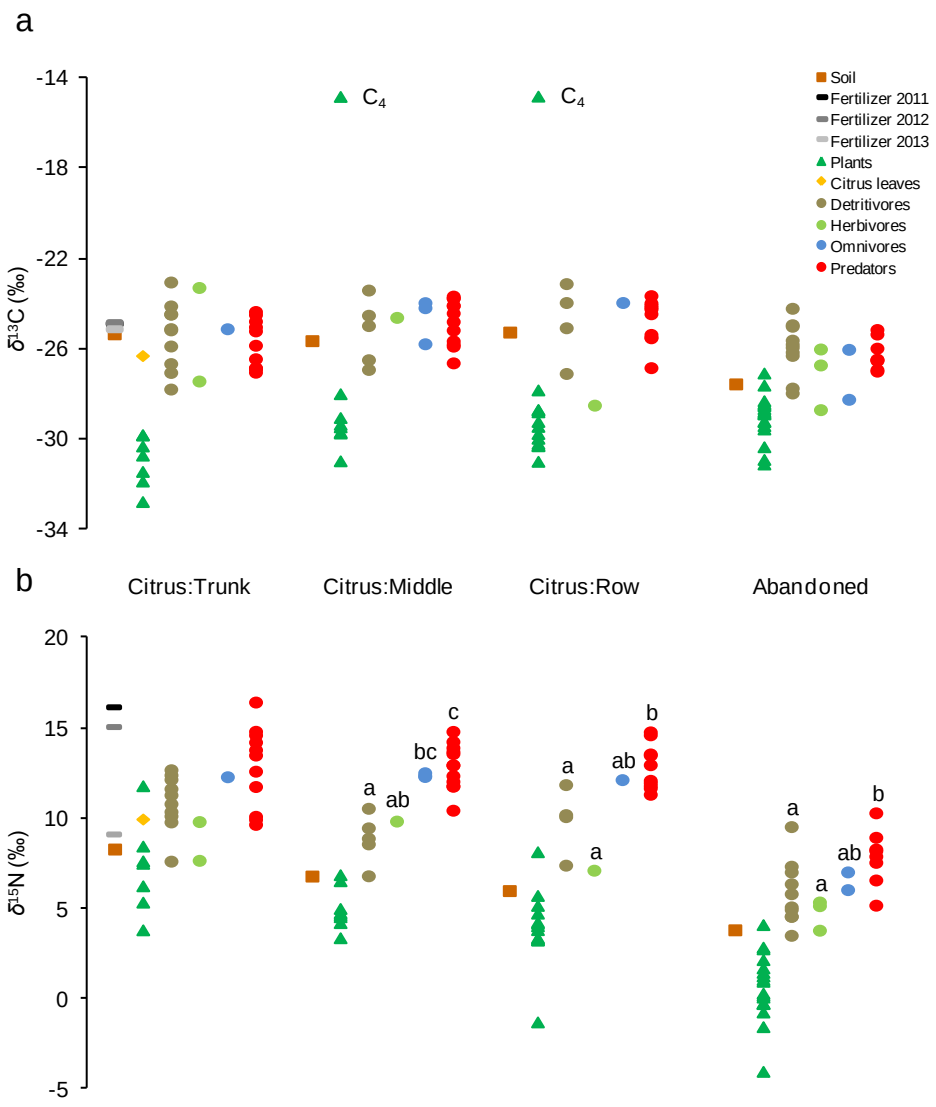
Macroinvertebrate community paralleled the $\delta^{13}C$ depletion of soil from the citrus grove to the abandoned field. Among plant species, the lowest $\delta^{13}C$ was found in Trunk, in *Rubia peregrina* (32.7‰) (Rubiaceae), whereas the highest one (14.7‰) was that of the C_4 grass *Cynodon dactylon*, present in Middle and Row. In all treatments no differences in $\delta^{13}C$ were found between trophic guilds (Fig. 4a).

Macroinvertebrate community paralleled the $\delta^{15}N$ depletion present in both soil and plants. However, while soil and plants decreased in $\delta^{15}N$ gradually at increasing distances from the tree trunk, in the macroinvertebrate community this depletion was only noticeable at a mesoscale (citrus grove vs abandoned field). The fertilizer applied near the tree trunk was always enriched in ^{15}N (2011: 16.1‰; 2012: 15.0‰; 2013: 9.1‰) with respect of soil in Trunk (8.3‰). Among plant species, the highest $\delta^{15}N$ was found in Trunk, in *Sonchus oleraceus* (11.8‰) (Compositae), whereas the lower ones were found in the abandoned field (*S. oleraceus*, -4.0‰; *Trifolium campestre*, -1.5‰ (Leguminosae)). Although no differences in $\delta^{15}N$ were found between trophic guilds in Trunk, in the rest of treatments there was a gradual pattern, yet overlapping, of $\delta^{15}N$ increase from detritivores to predators (Fig. 4b).

Fig. 4 a) $\delta^{13}C$ and b) $\delta^{15}N$ (arithmetic mean) of environment (soil, fertilizer, plants, citrus leaves) and macroinvertebrates classified in trophic guilds (detritivores, herbivores, omnivores, predators). For plants and macroinvertebrates each point represents one species. For macroinvertebrates within each treatment, shared letters or no letters mean no differences in δ values between trophic guilds ($P > 0.05$). Due to a lack of replicates no comparison could be made between herbivores and omnivores in Citrus:Row.

Fig. 4


a
-14
-18
-22
-26
-30
-34
δ13C (‰)
C4
C4
Soil
Fertilizer 2011
Fertilizer 2012
Fertilizer 2013
Plants
Citrus leaves
Detritivores
Herbivores
Omnivores
Predators
b
Citrus:Trunk
Citrus:Middle
Citrus:Row
Abandoned
20
15
10
5
0
-5
δ15N (‰)
a
ab
bc
c
a
a
ab
b
a
a
ab
b

Food web structure

Differences in macroinvertebrate community composition led us to delimit two food webs within the citrus grove (Trunk and Middle+Row), whereas different macroinvertebrate isotopic signature in the abandoned field also denotes and independent food web (Abandoned) (Table 1).

Table 1 Summary of the findings made in terms of spatial variability in community composition and stable isotope signatures. Same colour among treatments mean no differences between them. For isotopic signatures darker hue mean higher value. Macroinvertebrate community composition data from the abandoned field was excluded in the analysis (see Materials and Methods section).

		Citrus:Trunk	Citrus:Middle	Citrus:Row	Abandoned
Community composition	Plants				
	Macroinvertebrates				Not analized
Soil	$\delta^{13}C$				
	$\delta^{15}N$				
Plants	$\delta^{13}C$				
	$\delta^{15}N$				
Macroinvertebrates	$\delta^{13}C$				
	$\delta^{15}N$				

Within the citrus grove, soil $\delta^{13}C$ and $\delta^{15}N$ (covariates) did not affect macroinvertebrate community isotopic signatures (pseudo-$F_{1,212}$ = 1.05, P = 0.32; pseudo-$F_{1,212}$ = 0.01, P = 0.91; respectively). However, once isotopic signatures were corrected by their isotopic baselines, differences in $\delta^{13}C$ between treatments arose (pseudo-$F_{2,212}$ = 6.00; P = 0.0036), being Trunk depleted in ^{13}C with respect of Middle and Row (t = 2.77, P = 0.0063; t = 2.04, P = 0.045; respectively), with no differences between Middle and Row (t = 0.67, P = 0.51). In contrast, no differences in $\delta^{15}N$ between treatments persisted (pseudo-$F_{2,212}$ = 0.15, P = 0.86). On the mesoscale (citrus grove vs abandoned field), soil $\delta^{13}C$ and $\delta^{15}N$ affected macroinvertebrate community isotopic signatures (pseudo-$F_{1,297}$ = 6.63, P = 0.0063; pseudo-$F_{1,297}$ = 113.71, P = 0.0001; respectively). After controlling by these covariates the effect of treatment on $\delta^{13}C$ disappeared (pseudo-$F_{1,297}$ = 0.70; P = 0.44), but persisted for $\delta^{15}N$ (pseudo-$F_{1,297}$ = 22.31, P = 0.0001), indicating that macroinvertebrates from the citrus grove were enriched in ^{15}N with respect of those from the abandoned field.

Dual analysis of $\delta^{13}C$ and $\delta^{15}N$ allowed to establish nine trophic groups in each food web. In Trunk (Fig. 5d) the food web consisted in 4 trophic groups of detritivores, 2 of herbivores, 1 of omnivores and 2 of predators. Middle+Row food web (Fig. 5e) presented 3 trophic groups of detritivores, 2 of herbivores, 1 of omnivores and 3 of predators. Finally, the abandoned field food web (Fig. 5f) had 3 trophic groups of detritivores, and 2 of herbivores, omnivores and predators. Macroinvertebrates spanned through 5.8 trophic levels in Trunk, 5.4 in Middle+Row and 5 in the abandoned field food web. Although in all food webs the vast majority of macroinvertebrates are close to that $\delta^{13}C$ of soil (Fig. 5a, b and c), some trophic groups (or at least species) of herbivores and detritivores presented either higher or lower $\delta^{13}C$.

For trophic diversity, Middle+Row food web was that with a higher diversification at its base (higher δ^{13}C range), whereas trophic lenght (δ^{15}N range) decreased from the Trunk to the abandoned field. Trophic niche width (total area in the δ^{13}C-δ^{15}N space) was higher in the citrus grove food webs than in the abandoned field one. Average trophic diversity (mean distance of each species to the community centroid) was higher in Trunk than in the rest of the food webs. For trophic redundancy, the abandoned field food web presented higher density of species (MNND) and higher evenness of their distribution (SDNND) than those from the citrus grove (Table 2). Although certainly credibility intervals overlapped to a greater or lesser extent between metrics (ESM Fig. S1), the probabilities of the bayesian models indicated that there is a trend in that trophic diversity in Trunk ≥ Middle+Row > Abandoned and, for trophic redundancy, Abandoned field ≥ Citrus grove (Table 2).

549 **Fig. 5** In a), b) and c) $\delta^{13}C$ and $\delta^{15}N$ (mean ± SE) of macroinvertebrates, plants, soil,
550 and other environmental items are provided for each food web. In d), e) and f)
551 macroinvertebrates of the same trophic guild are grouped into ellipses of isotopically
552 similar species, conforming trophic groups of detritivores (brown), herbivores (green),
553 omnivores (blue) and predators (red) in each food web. Each trophic group is labelled
554 (e.g. d1 = trophic group 1 of detritivores). $\delta^{15}N$ for each trophic level (TL) is indicated
555 on the y-axis. As there were isotopic differences between soil from Middle (M) and
556 Row (R), both are represented in b). For coherence in graphic representation, δ values of
557 the plant *Cynodon dactylon* (Gramineae, C_4) in b) were omitted ($\delta^{13}C$: -14.8‰, $\delta^{15}N$:
558 4.0‰).
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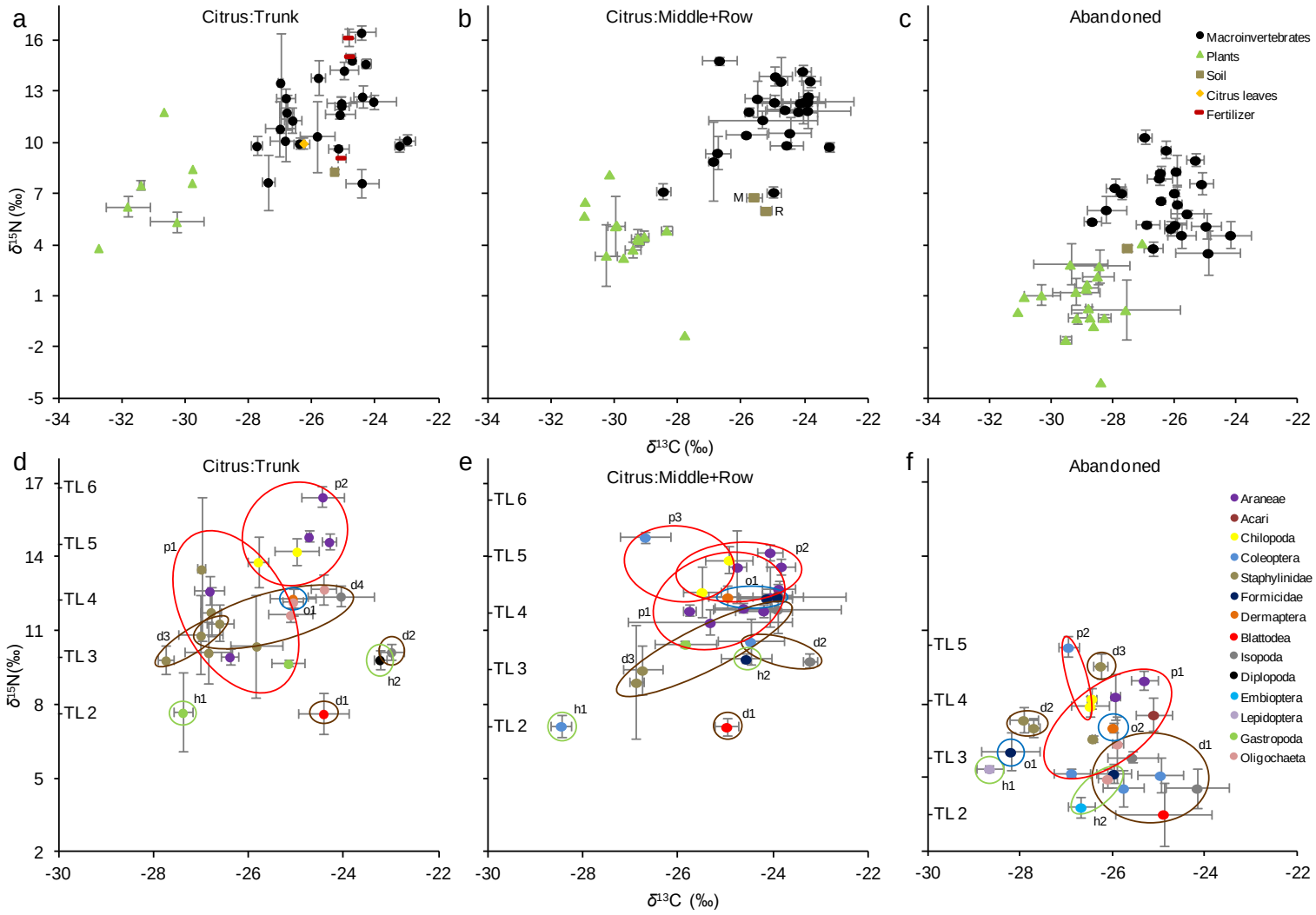
a
Citrus:Trunk
b
Citrus:Middle+Row
c
Abandoned
Macroinvertebrates
Plants
Soil
Citrus leaves
Fertilizer
δ15N (‰)
δ13C (‰)
d
Citrus:Trunk
e
Citrus:Middle+Row
f
Abandoned
TL 6
TL 5
TL 4
TL 3
TL 2
Araneae
Acari
Chilopoda
Coleoptera
Staphylinidae
Formicidae
Dermaptera
Blattodea
Isopoda
Diplopoda
Embioptera
Lepidoptera
Gastropoda
Oligochaeta

Fig. 5

577 **Table 2** Mean (in ‰, except for total area (‰^{2})) of the community-wide metrics of
578 trophic diversity and trophic redundancy calculated for each food web using a bayesian
579 approach. Probabilitiy that a metric is higher in a food web than in another is given.

Type	Metric	Food web			Probability that		
		Trunk	Middle+Row	Abandoned	Trunk> Middle+Row	Trunk> Abandoned	Middle+Row > Abandoned
Trophic diversity	δ^{13}C range	5.5	6.6	5.5	0.272	0.535	0.728
	δ^{15}N range	10.1	8.8	7.6	0.761	0.923	0.817
	Total area	34.9	36.7	25.3	0.447	0.873	0.891
	Mean distance to centroid	2.5	2.2	2.1	0.820	0.918	0.677
Trophic redundancy	Mean nearest neighbour distance (MNND)	0.9	0.9	0.8	0.513	0.745	0.740
	Standard deviation of nearest neighbour distance (SDNND)	0.7	0.8	0.5	0.337	0.746	0.863

580 See ESM Fig. S1 for a graphic representation of the credibility intervals for each metric in each food web.
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598 **Discussion**

599 *Spatial variability in community composition*

600 Within the citrus grove, the macroinvertebrate community near the trunk differed from
601 that located farther away, mainly because of a higher number of detritivores (*e.g.*
602 Aleocharinae staphylinid beetles). It is known that decomposer communities are most
603 developed in organic soils (Anderson 1975), and therefore they benefit from organic
604 farming (Birkhofer et al. 2008). Thus, the organic manure applied near the tree trunk
605 may be fostering faunal decomposers. In addition, irrigation below the canopy may
606 increase the abundance of herbivores by enhancing plant quality (Pérez-Fuertes et al.
607 2015), as indicated by the concentration of diplopods and snails in Trunk. Given that
608 low spatial variability in food web composition in homogeneous forests are supposed to
609 be related to a low spatial variability in organic matter turnover (Berg and Bengtsson
610 2007), the striking small scale at which differences in macroinvertebrate community
611 appeared (decimetres) probably reflects the scale at which differences in soil organic
612 matter content appear (Trunk: 7.7±0.6%; Middle+Row: 3.9±0.3%).

613 Plant community followed a predictable distribution common to agricultural and ruderal
614 environments in the Mediterranean region (Folch and Franquesa 1984). *Parietaria*
615 *officinalis* (Urticaceae) is a nitrophilous plant most abundant near the trunk, where the
616 fertilizer is applied. In contrast, between tree rows is common to find communities
617 dominated by annual weeds and perennial grasses such as *Cynodon dactylon*.
618 Abandoned crops often become barren land, with progressive enrichment in nitrogen
619 and high soil compaction. These environments tend to be dominated by ruderal species
620 such as *Dittrichia viscosa* and *Carduus pycnocephalus* (Compositae).

621 *Spatial variability in environmental stable isotope signatures*

622 Water stressed plants are enriched in ^{13}C due to an increase in water use efficiency, and
623 C_4 plants present higher $\delta^{13}C$ (~ -14‰) than C_3 plants (~ -27‰) (Marshall et al. 2007).
624 We suggest that plants near the trunk had lower $\delta^{13}C$ than plants from the other
625 treatments due to the effect of irrigation. In addition, *Cynodon dactylon*, a C_4 grass
626 present in Middle+Row, broadened this difference (ESM Table S3). Since soil $\delta^{13}C$
627 integrates plant material $\delta^{13}C$ over time (Balesdent et al. 1993), higher $\delta^{13}C$ and wider
628 differences between soil and plant $\delta^{13}C$ in the citrus grove might be a consequence of a
629 gradual substitution of C_4 for C_3 plants. While in the past the plant community in the
630 citrus grove was dominated by *Portulaca oleracea* (Portulacaceae, C_4) (Cañellas,
631 personal communication), now is dominated by C_3 grasses, with *C. dactylon*
632 representing only the 7.3% of total biomass.

633 Plants are assumed to reflect bulk soil $\delta^{15}N$, and while ^{15}N-enriched fertilizers enrich
634 soil in ^{15}N, nitrogen-fixing organisms reflect atmospheric $\delta^{15}N$ (0‰) (Evans 2007,
635 Marshall et al. 2007). Fertilizer applied near the trunk was on average 5.1‰ higher than
636 soil. Thus, decreasing values of soil and plant $\delta^{15}N$ from the tree trunk to the abandoned
637 field are supposed to be related to the effect of the fertilizer. Moreover, legumes (with
638 N-fixing symbionts) were abundant in the abandoned field (26.4% of all biomass) and
639 might slowly deplete soil $\delta^{15}N$ by long-term litter deposition.

640 *Stable isotope signatures of macroinvertebrates*

641 Isotopic composition of ecosystems affects the isotopic composition at the base of the
642 food web (Post 2002), which in turn affects the entire community (Ponsard and Arditi
643 2000). While less mobile organisms may reflect the isotopic signal of their
644 environment, wider foraging area are expected to lead in the integration of some of the
645 environmental isotopic variability (Bearhop et al. 2004). Macroinvertebrate community

mirrored the depletion in $\delta^{13}C$ and $\delta^{15}N$ of soil from the citrus grove to the abandoned field, suggesting that these communities are physically and, therefore, trophically isolated from one another.

The small differences in $\delta^{13}C$ between trophic guilds in all treatments and their close relation to the isotopic soil signature suggests a generalized common pathway of energy flux from soil organic matter to detritivores to predators, common in soil food webs (*e.g.* Halaj et al. 2005). However, the wide range of $\delta^{13}C$ (4.9‰ ± 0.3) suggests other potential pathways like that related to primary production that herbivores might be exploiting.

In contrast, there was a clear pattern of ^{15}N enrichment from detritivores to predators. This means that classifying macroinvertebrates into a priori trophic guilds can help to understand the food web structure, since, as stated by Layman et al. (2007), "disparate feeding pathways may lead to the same position of two or more species in niche space". However, there was a large intraguild variability, reflected by $\delta^{15}N$ range in detritivores (5.4±0.3‰) and predators (5.4±0.7‰). Thus, this classification would be useful as long as taxonomic resolution is high (Mestre et al. 2013). This great intraguild variability and the overlap between trophic guilds corroborates the idea that soil food webs are formed by a trophic continuum rather than by well defined trophic levels (Scheu and Falca 2000, Ponsard and Arditi 2000), containing functional groups within trophic guilds (Oelbermann and Scheu 2010). Thus, these food webs are dominated by two trophic levels (detritivores and predators) with unspecific feeding habits and high levels of omnivory (Scheu and Setälä 2001).

Food web structure: trophic shifts

669 Food webs are often ascribed to traditional ecosystem units (*i.e.* community webs *sensu*
670 Cohen 1977). However, we were able to define two food webs within the citrus grove
671 just a few decimetres apart. Evidences of food web division stem from differences in
672 community composition, different top predators at each food web (ecotrophic module;
673 Cousins 1990) and differences in corrected δ values (see below). Nevertheless, since
674 these food webs shared 26% of total species (probably the most mobile ones) total
675 impermeability is not expected (see Post et al. 2007).

676 Post (2002) outlined the necessity to consider the food web baseline to separate
677 community isotopic changes due to the baseline itself from those due to shifts in food
678 web structure. Corrected δ values suggest that macroinvertebrates from the citrus grove
679 are feeding on higher trophic positions than those from the abandoned field. We
680 hypothesize that higher total abundance of decomposers near the trunk is driven by
681 detritus subsidies from the organic fertilizer (Polis et al. 1997), ultimately leading to an
682 increase in trophic lenght (productive space hypothesis; Schoener 1989) and therefore in
683 trophic diversification (Hutchinson 1959). Increased productivity may in turn allow
684 species of the same trophic level to avoid competition (Hairston et al. 1960), enabling
685 them in turn to feed on higher trophic positions (protein-rich diets) and rely less in
686 omnivory or plant-based resources. This hypothesis is reinforced by two evidences.
687 First, by the trend in decreasing trophic diversity from the citrus grove to the abandoned
688 field (generally, Trunk $\geq$ Middle+Row > Abandoned) and in the higher trophic
689 redundancy in the abandoned field (generally, Abandoned field $\geq$ Citrus grove), which
690 mean higher trophic niche overlap and therefore higher competition among species
691 (Layman et al. 2007). Second, by the fact that even the seed harvester ant *Messor*
692 *barbarus* is enriched in ^{15}N in the citrus grove in comparison to the abandoned field. In
693 the citrus grove these ants were observed carrying dead animals to their nests, a

694 behaviour not observed in the abandoned field. *Messor barbarus* is thought to feed
695 preferentially on seeds because it is a more abundant resource and decreases
696 interspecific competition (Fernández-Escudero and Tinaut 1993).

697 Corrected δ values also show that within the citrus grove, Trunk food web was depleted
698 in ^{13}C in comparison to Middle+Row food web, suggesting that nutrient and water
699 subsidies from fertilization and irrigation may enhance plant quality and additional
700 energy pathways related to plant and fungal resources (see below).

701 *Food web structure: trophic groups of arthropods*

702 For detritivores, *Loboptera decipiens* (Blattodea) appears to be the primary decomposer
703 at the base of all food webs (d1; see Fig. 5), with similar isotopic values than that of
704 soil. While in the citrus grove food webs the rest of detritivores act as secondary
705 decomposers (d2-d4), in the abandoned field even the same species seem to act as
706 primary decomposers (d1), probably as a consequence of a slowing in decomposition
707 processes (Seeber et al. 2005). In all food webs staphylinid beetles are the group of
708 detritivores with lower $\delta^{13}C$ values, suggesting that they rely on decomposed fractions
709 of plant material such as litter, which is enriched in ^{13}C in comparison to fresh material
710 (Tiunov 2007). While in Trunk *Medon* sp. may act as both primary and secondary
711 decomposer (d4, TL 2-3), in the abandoned field might be a saprophague (d3, TL 4).
712 Within the citrus grove the rest of detritivores present higher $\delta^{13}C$ values and consist in
713 secondary decomposers represented by earthworms (only in Trunk) and isopods,
714 potentially feeding on soil organic matter and detritus. In all food webs the isopod
715 *Armadillidium vulgare* have the highest $\delta^{13}C$ value, which may reflect its preference for
716 feeding on faecal material (Zimmer 2002), known to be enriched in ^{13}C (DeNiro and
717 Epstein 1978). The myrmercophilous beetle *Oochrotus unicolor* (Histeridae) presents a

similar isotopic signature than the seed harvester ant *Messor barbarus*, suggesting a high reliance on the ant's food resources and remains.

Predators form two clear distinct groups in Trunk food web. The first group (p1; see Fig. 5), composed by predatory staphylinids and lyniphiid spiders (average body length 2.1 mm), is potentially exploiting the additional energy channel, preying upon litter feeder staphylinids and probably non-analyzed mesoarthropods such as fungal feeder collembola, which have low δ^{13}C values and are present in the diet of lyniphiids (Pollierer et al. 2009; Piñol et al. 2014). The staphylinid beetle *Philonthus* sp. may as well prey on multiple trophic levels and even engage cannibalism given its extraordinary high variance in δ^{15}N. Although the herbivorous snail *Cornu aspersum* is a potential prey for the predatory snail *Rumina decollata* (Deckle and Fasulo 2001), due to high differences between their δ^{13}C values the later might be feeding on other plant or soil-based resources. The second group (p2) is formed by chilopods and bigger spiders (average body length 11.6 mm), potentially preying on secondary decomposers below them and non-analyzed enchythaeids, which present high δ^{13}C values (Schmidt et al. 2004). Since this predator group are one trophic level above the former, intraguild predation must also be considered, even for the spider *Nemesia* sp. (the macroinvertebrate top predator, TL 6) within its trophic group. However, while in this food web intraguild predation might be restricted to the bigger species and may be less common due to high prey availability (Wise et al. 1999), in Middle+Row there are evidences that it is a pervasive feature: although prey subsidies from Trunk may allow the existence of a diversified predator community (Polis et al. 1997), there is a generalized scarcity of potential food sources, high overlap between trophic groups (p1-p2) and trophic niches of species, and mean ^{15}N enrichment with respect to detritivores is 3.1‰, which is more than one trophic transfer. In the abandoned field food web,

743 predator structure layout is similar to that of the citrus grove, but simpler. It has been
744 proposed that feeding in lower trophic positions may reflect a simple community, where
745 lower rates of predation may occur (Gibb and Cunningham 2011). Therefore, low ^{15}N
746 enrichment from detritivores to predators (2‰, as in Trunk) might suggest high levels
747 of omnivory (Cabana and Rasmussen 1994) rather than a generalized lack of intraguild
748 predation. For instance, *Silpha puncticollis* (Coleoptera: Silphidae), which present the
749 lowest $\delta^{15}N$ among predators (5.2‰), can shift its feeding habits depending on the
750 availability of resources (Blas 1987). *Kissister minimus* (Coleoptera: Histeridae), the
751 macroinvertebrate top predator in Middle+Row and Abandoned food webs, occupy a
752 very different trophic position compared to the rest of predators. Although it might be
753 engaging intraguild predation, potential food sources are difficult to discern with the
754 available data.

755 Omnivorous arthropods are always placed between detritivores and predators, which is
756 consistent with their animal and plant-based resources utilization. An exception is the
757 ant *Plagiolepis pygmaea* in the abandoned field food web, which has a very low $\delta^{13}C$
758 value, probably reflecting an over-reliance on plant-based resources in an environment
759 poor in potential preys, a feature previously reported in omnivorous ants (Tillberg et al.
760 2007).

761 According to their trophic guild, herbivores generally presented the lowest $\delta^{13}C$ values,
762 *i.e.*, those closer to the plants. However, the diplopod *Polydesmus* sp. in Trunk, the seed
763 harvester ant *Messor barbarus* in Middle+Row and Abandoned, and the embiopteran
764 *Haploembia solieri* in Abandoned, presented higher $\delta^{13}C$ values, suggesting that they
765 might be feeding on ^{13}C-enriched non-analyzed plant compounds (see Pollierer et al.
766 2009).

Concluding remarks

In the studied agroecosystem, the gradient in soil organic matter content (fertilizer) and water availability (irrigation) from the tree trunk in the citrus grove to the adjacent abandoned field could be demonstrated by soil and plant isotopic signatures. This spatial variability is thought to be the main driver of changes in food web structure. Within the citrus grove, detritus and water subsidies may be fostering faunal decomposers and an additional plant/fungal-based energy channel near the tree trunk, in comparison to increasing distances. Compared to the abandoned field, increased prey availability in the citrus grove may in turn allow higher trophic diversification and let the macroinvertebrate community to feed on higher trophic positions.

Food web studies must take into account within-habitat heterogeneity, since our study highlights that even macroinvertebrate communities can show differences in composition and trophic structure at scales of decimetres. Thus, such small scales should be considered when determining sampling scales and food web-related ecosystem processes.

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Conflict of Interest: The authors declare that they have no conflict of interest.

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